

OBSERVATIONS ON THE EARLY STAGES IN THE  
DEVELOPMENT OF THE EMU (*DROMLEUS NOVÆ-  
HOLLANDIÆ*.)

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(PLATES VIII.-XV.)

The number of works and papers on the development of birds is so great that an apology would almost seem to be required for adding one more to the list. But while the common fowl, pigeon, sparrow, thrush, nightingale, red-breast, canary, tit, lapwing, thick-knee, plover, duck, goose, tern, sea-gull, and some others have been dealt with as regards their embryology in whole or in part, there are no recorded observations on the development of any member of the great Ratite or Struthioid sub-class; and I have therefore thought it worth while to place on record the results of a study of the early development of the Emu, on which I have been engaged during the last few months.

In what follows there may seem to be a little which may be regarded as a threshing-out anew of a well-threshed subject; but when it is considered how wide is the diversity of opinion even at the present time among embryologists as to the significance of certain of the facts of avian embryology, it may be acknowledged that the reconsideration of certain of these in the case of a type so widely removed from those ordinarily studied may be of some value.

I have to acknowledge here my great indebtedness to my friends Dr. R. L. Faithfull, of Lyons Terrace, Sydney, and Dr. Eric S. Sinclair of Gladesville Asylum, to whose kindness I owe my supply of material for this research.

It will be superfluous to preface the account of these observations with any general resumé of previous investigations and theories on avian embryology. This has been done with sufficient thoroughness from different standpoints by Kölliker, Balfour, Wolff, Koller, Duval, and others ; and I shall merely allude in their place to such points in the literature of the subject as are suggested by these observations on the emu.

For comparison I have used only the common fowl ; and for the most part the methods employed were the methods of treatment and preparation followed in the study of that bird\*, with such modifications as were rendered necessary by the larger size and different consistency of the yolk. The eggs of the emu were incubated at a temperature of from 35° to 40° C. Under this treatment there was a very considerable range of variation in the stage to which a given period of incubation would bring different eggs ; but there were in one of the two sets of eggs at my disposal no indications of any abnormalities, and there is every reason to believe that the temperature employed was about the natural one. The period of incubation of the emu is three months, as contrasted with the four weeks of the fowl, and the time which elapses before any one of the principal events of the development takes place in the former is nearly a corresponding multiple of the time which elapses in the case of the chick.

An average egg of the emu is twenty-one ounces in weight, and measures rather over four inches in length by three and a half in breadth. Of these about forty may be laid in a season ; when about fifteen have been laid the male bird proceeds to incubate them, and perseveres in this duty until the first set of young ones are hatched, when he is succeeded by the female bird, which has now for some time ceased laying.

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\* See particularly Dr. C. O. Whitman's admirable "Methods of Research in Comparative Anatomy and Embryology," and the introductory part of the memoir by Duval, quoted below (XII.).

The various parts of the egg have precisely the same relations as in the fowl; the white is rather less in proportion to the yolk; but there is no other difference of importance. The yolk is about seven and a-half centimetres in its long, and seven in its short diameter; the long axis coincides with that of the egg; and usually there are discernible a broad end and a narrow end corresponding with the broad and narrow ends of the egg itself.

The embryo was usually found to lie with its long axis at right angles with the long axis of the yolk and of the egg; but not unfrequently the position was oblique, though never longitudinal.

The unincubated blastoderm was of nearly the same size and appearance as in the fowl, and was not made the subject of special examination. In eggs incubated for from about forty-seven to fifty hours the entire blastoderm was about a centimetre in diameter; the area pellucida was two millimetres in diameter, and with a dark patch, the 'embryonic shield,' in the middle.

A blastoderm of fifty-one hours was the earliest of which a thorough study was made. The entire blastoderm was a centimetre in breadth and the area pellucida three millimetres in its greatest diameter. The area pellucida presented two regions—an anterior which was rounded and rather broader than long, and a posterior, which had the appearance of a very short and narrow bay of the anterior part. This posterior bay (the 'Zuwachsstück' of His) is the commencement of the primitive-streak region, and presents an indistinct dark axial band which is the commencement of the primitive streak. In no part was there a trace of a primitive groove. When examined in sections this blastoderm was found to consist throughout of only two completed layers—an upper and a lower. In the anterior larger part of the area pellucida these are separated throughout by a well-marked interval. In the posterior bay they are confluent along the middle line—forming the primitive streak. A little distance in front of the anterior end of the primitive streak the lower layer presents in the middle a slight thickening of no great extent. This is the earliest rudiment of

the so-called 'head-process' (Kopffortsatz) of the primitive streak, the significance of which will be discussed later on. It begins very gradually in front and passes behind without interruption into the primitive streak. In this 'head process' as well as in the region of the primitive streak (plate XII. fig. 9) the lower layer presents below, here and there, a flattened cell. These flattened cells are very far at this stage from forming a complete layer in this part of the blastoderm; but there can be no doubt that they are the first-formed elements of the definitive hypoblast produced by modification of some of the lower-layer cells. In the middle of the primitive-streak region those cells are more numerous, and for a short distance form a complete layer; but not even there are they separable from the rest of the lower layer except by their shape. The two lateral halves of the primitive streak are completely coalescent, there being at no point any indication of the "suture" or of the canals which are to be seen at a later stage. The primitive streak is continued backwards for some little distance over the area opaca as a thickening of the epiblast. It is noteworthy that there is no appearance of a 'sickle', which if it existed as in the chick and some other carinate birds, would be recognisable in this series of sections.

In a specimen which had been incubated for seventy hours, in which the entire blastoderm was about two centimetres in diameter, the area pellucida (plate VIII, fig. 1), four or five millimetres in length, had attained a shape very unlike that which it presents at this period in the fowl. It consisted, as in the previous stage, of two parts—an anterior part, which was nearly circular, and a posterior part, which had the form of a narrow prolongation of the anterior part. This posterior prolongation is now of considerable length. On its surface, and extending forwards towards the centre of the rounded part of the area pellucida, was the primitive streak, having running along its axis a well-developed primitive groove, which became lost behind on the inner margin of the area opaca. The primitive streak ended in front in a not

very well-defined border, in front of which is a transverse dark space with a convex anterior border and shading off behind into the primitive streak proper.

In the anterior part of the area pellucida of this specimen, as seen in sections, there are only two layers—epiblast and lower layer. The cells of the latter have not here yet taken on their flattened form, but are irregular and amoeboid, many of them thickly loaded with granules, arranged in a single layer. The epiblast consists in the middle of several layers of cells containing in many instances large granules: at the sides it consists of a single layer. The mesoblast has not yet extended into this region. As we pass backwards the cells of the lower layer gradually lose their amoeboid character and become more flattened, though still irregular in shape—the change in their form beginning in the middle line.

The “head-process” (plate XII., fig. 10) is now larger than in the preceding stage, and its cells have assumed an irregular, sometimes stellate, form; here and there, as before, there is a flattened cell foreshadowing the hypoblast, but the majority of the cells are manifestly assuming the form of stellate mesoblast cells. Behind, as in the last stage, the head-process passes without interruption into the axial plate. In the primitive streak itself (plate XII., figs. 11 and 12) there is the usual axial plate continuous with the surface epiblast, its lateral wings extending outwards between the epiblast and the hypoblast, which latter has now in this region become developed into a continuous layer of somewhat flattened cells. The mesoblast extends outwards far beyond the termination of the hypoblast in the germinal wall.

In the hinder part of the primitive streak region (fig. 13) there is below the primitive groove what appears like an imperfectly united longitudinal cleft or suture in the axial plate. The hypoblast below this is continuous across the middle line, but in the centre, just below the “suture,” the ordinary hypoblast cells are replaced by a large cell filled with coarse granules. Though this is a fresh formation since the last stage, we have here an

indication of the lips of the anterior part of the blastopore, the connection of which with the marginal portion has long been lost.

Below the blastoderm proper in this specimen are a number of large cells (*n*, figs. 10-12) mostly of rounded form, filled with large granules. These are present also in the last stage, but not so definitely arranged. In the blastoderm now being described they become very numerous below the head-process, where they form a broad axial band. A few of them are to be observed in the substance of the lower layer itself. In the primitive-streak region they are arranged for the most part in a double row, one running along below each lateral limit of the developing mesoblast. These are evidently the bodies termed formative cells by Balfour, globules of Ecker by Duval. They have been found to be derived from segmentation nuclei which appear on the floor of the segmentation cavity. It would seem probable from their arrangement as above described that their special function is the conveyance of nutriment directly or through the cells of the hypoblast to the developing mesoblast. At a stage when the mesoblast is well established they are no longer traceable.

Blastoderms resembling that above described, were obtained several times; with slight variations in minor points all presented the peculiar narrow posterior prolongation of the area pellucida forming the primitive streak region.

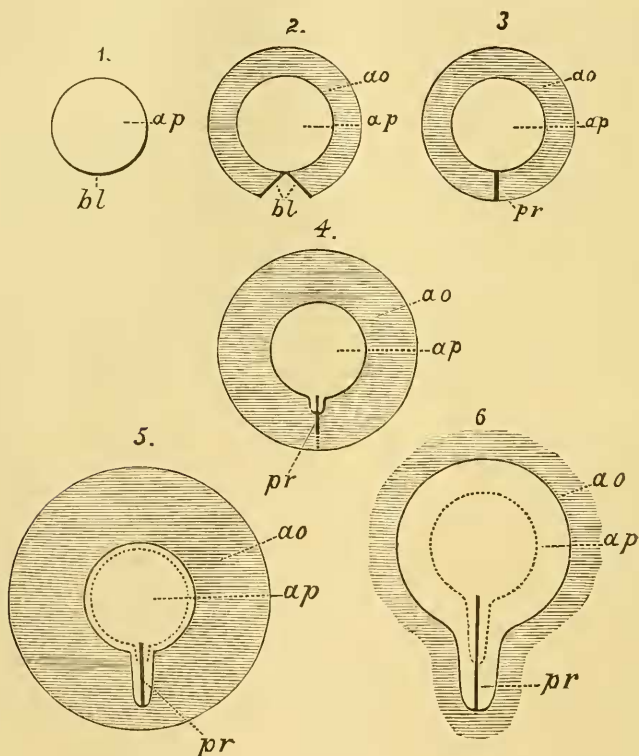
In a specimen incubated for sixty-six hours (plate VIII, fig. 2,, the posterior prolongation was broader and less strongly marked off from the rest of the area pellucida; the head-process had a more definite outline, and there was a semicircular groove which marked the position of the anterior boundary of the future medullary plate. On examining this blastoderm in a series of transverse sections, it is found that the head-process is much larger than in the preceding stage. It begins very gradually in front as a proliferation of lower-layer cells; but attains a considerable thickness behind. In front there is no hypoblast distinguishable in it; but behind a hypoblastic layer becomes more evident, though not sharply marked off in any part. Behind, the head-process

passes without interruption into the axial plate, and here a well-formed hypoblast becomes first clearly marked off. In the region in front of the primitive streak and behind the crescentic groove—the region that is of the future medullary plate—the epiblast is thicker than in the surrounding parts of the blastoderm, and its cells have a more regular form. The suture in the primitive streak referred to above, has now altogether disappeared, and the two halves are closely united throughout their length.

A study of the three stages which have been described, renders it evident that the primitive streak cannot grow forwards from the posterior border of the *area pellucida*, as it is generally described as doing; but that it is formed from before backwards simultaneously with an extension backwards in the form of a narrow bay, of the *area pellucida*. The sub-germinal cavity, that is to say, sends an axial bay backwards, the posterior part of the germinal wall bends backwards at the same time along the border of this bay, and there is thus formed a narrow posterior prolongation of the *area pellucida*, on the surface of which the primitive streak appears. Its first rudiment is apparently an axial thickening of the upper layer on the region of the *area opaca* which is to be converted into this bay; and as the bay extends back the lower layer also thickens, the two thickenings uniting. The *area pellucida* has meantime been extending itself by growth in all directions, with the result that the anterior end of the primitive streak comes to be situated not far behind the middle of the anterior circular part of the *area pellucida*. That there is, however, a certain forward growth of the anterior end of the streak after it has become formed, seems probable when we compare figures 1 and 2 in plate; it is, however, of much less extent in the emu than in the fowl.

The accompanying woodcuts are designed to illustrate the history of the formation of the primitive streak in the emu. Only a part of this history is traceable in the ontogeny of the individual, and much less than at the outset I had hoped to find,—little more in fact than in the chick, save that the mode of growth of the

primitive streak region is more readily traceable in the emu, and that the relations of the primitive streak are not complicated by the formation of a sickle or of a sickle-groove. The earliest stages in the development of the blastoderm I assume to be similar to those of the embryos of carinate birds as described by Duval.\* Fig. 1



represents a blastoderm of a stage in which the continuity of upper and lower layers (represented by the thickened line *bl*) has become restricted to the posterior border. Fig. 2 represents diagrammatically the infolding of this border by reason of the

\* XII. p. 100, &c.

rapid extension of the blastoderm in all directions. In fig. 3 the two halves of this border have come together to form the axis of the primitive streak. This stage, in which the lateral halves of the primitive streak, meeting along the middle line in a sort of suture, run from the posterior border of the area pellucida to that of the area opaca, has not been observed, and possibly does not occur in the ontogeny of any bird. In figure 4 the area pellucida is represented as beginning to send backwards a narrow prolongation, on the surface of which the primitive streak becomes revealed. The posterior part of the suture, *i.e.*, that part which traverses the area opaca, is not represented in the emu, so far as I have been able to ascertain, even by a posterior notch such as is not rare in the fowl\*; the primitive streak would appear in fact (in the history of the individual) to be formed on the surface of the area pellucida as the latter extends backwards, and to be only foreshadowed in the area opaca by a median thickening of the upper layer, which does not extend far back. The remaining two figures are intended to illustrate the manner in which, as pointed out by Duval, the anterior end of the primitive streak comes in its later stages to be situated so far forwards simply by the considerable extension of the area pellucida on all sides.

The 'head-process,' to which repeated allusion has already been made, has been, as regards its relations in the chick, the subject of some discussion. By Kölliker† it is described as being a prolongation forwards from the anterior end of the primitive streak; and, in accordance with his view of the origin of the primitive streak, he regards it as derived from the epiblast; he is of opinion that it probably gives rise to the whole of the head.

Gerlach‡ describes it as a thickening of the endoderm, and as separated from the cells of the primitive streak behind by an

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\* Whitman describes (XXXII) an abnormal blastoderm of the chick in which this line of coalescence is represented on the area opaca by a continuation backwards of the primitive groove to the posterior border.

† XXIV., p. 107.

‡ XVI., p. 45.

oblique cleft. There is no trace of any such break in any of my series of sections; the axial plate in fact is completely continuous with the head-process. It is very difficult, however, to say whether or not the thickening constituting the 'head-process' is brought about by an invasion of cells from the primitive streak. The former (which is more correctly described as *medullary plate of lower layer*) is continuous with the latter by a process of cells, but whether cells travel forwards through this process and add to the thickness is hardly capable of being decided. It seems probable that the 'head-process' is merely the continuation forwards for a short distance of that axial thickening of the lower layer, which, as above described, accompanies the formation of the primitive streak, and, except that it does not coalesce with the epiblast, the history of the lower layer is the same here as further back; a layer of flattened hypoblast is derived from the lowest of its cells, and the rest is converted into mesoblast.

It may be useful to sum up here the history of the formation of the mesoblast in the emu. When the primitive streak is first formed there are only two layers in the blastoderm. These two layers—upper and lower—both become thickened along the axial line of the area pellucida in its posterior prolongation, and there coalesce—the coalescence *plus* the thickenings constituting the primitivestreak. The thickening of the lower layer extends forwards a short distance in front of the anterior end of the primitive streak to constitute the 'head-process.' The lowermost cells of the lower layer about the time of the first appearance of the primitive streak begin to be differentiated into a series of flattened cells which afterwards unite to form a continuous layer of cells—the hypoblast. This becomes a complete layer much later in the region of the 'head-process' than in the region of the primitive streak. In the lateral parts of the area pellucida, where the lower layer is thin, its cells become entirely converted into the single layer of hypoblast cells. In the middle the cells which remain after the hypoblast has become formed go to form the earliest rudiment of the mesoblast; the hypoblast becomes separated from this rudimentary mesoblast, and the latter from

its close connection with the epiblast has the appearance, especially after the primitive groove has become formed, of being an outgrowth from an involution of the epiblast. The mesoblastic plates are formed by outgrowth from this primitive mesoblast of the primitive streak extending outwards between the epiblast and the hypoblast. The union of the primitive mesoblast with the epiblast in the axial line of the primitive streak being complete, it is very difficult to say that the epiblast has no share in the growth of the lateral plates ; probably the union exerts some influence on the activity of the primitive mesoblast cells ; but I think we may safely say in view of the facts adduced above, that the foundation of the mesoblast of the whole embryo is laid by the cells of the lower layer, and that no part of it up to this point is formed directly from the epiblast.

The above account of the formation of the mesoblast in the emu is in substance the same, so far as I can ascertain at second-hand from Koller's summary\*, as that put forward by His for the fowl. It is the view also maintained by Rauber†, by Disse‡, and by Duval§. On the other hand Kölliker|| regards the mesoblast as formed by ingrowth from the epiblast along the line of the primitive streak. Gerlach ¶ also describes the mesoblast as of epiblastic origin, and also Koller, who, however, regards the participation of the hypoblast as probable, but not certainly ascertained. Balfour\*\* maintains that part of the mesoblast of the primitive-streak region is derived from the epiblast.

In connection with this subject it has to be noted that the chick as described by Balfour and others, differs from the emu, in that

\* XXII. p. 202

† XXVIII.

‡ XI. p. 86.

§ XII. p. 115.

|| XXIV. p. 93, &c.

¶ XVI.

\*\* III.

in the former the hypoblast is present as a distinct layer in the hinder part of the area pellucida before the formation of the primitive streak, and it is this, apparently, that has given rise to the view so widely maintained that the mesoblast in the region of the primitive streak is mainly derived from the epiblast, or that the whole mesoblast is so derived.

During the ensuing few hours the blastoderm increases rapidly in size, its diameter nearly doubling itself in a comparatively short time ; the area pellucida, however, does not increase in dimensions in the same proportion. In a specimen which had been incubated for seventy-eight hours, the area-pellucida (plate IX., fig. 3) was still only about four millimetres in length. A little in front of the middle is a rounded elevation, the head elevation, which slopes away gradually behind, but in front is circumscribed by a well-defined strongly convex border—the border of the head-fold. Running along the axis of this elevation is a narrow and deep fissure, which reaches from close to the convex anterior border to about the middle of the area pellucida, ending apparently abruptly at both ends. This fissure—the medullary groove—is bounded by a pair of low rounded medullary folds which decrease in height gradually behind. A little distance behind its posterior end is the beginning of a second longitudinal fissure, the primitive groove, which appears to begin in front in a slight enlargement, but loses itself insensibly behind.

In the region in front of the head-fold the blastoderm still consists only of two layers of cells—the epiblast and a single layer of irregular amœboid cells—the mesoblast not appearing in this region till somewhat later. Immediately in front of the head-fold the hypoblast takes on its definite flattened character, and in the head-fold itself the mesoblast makes its appearance and extends a considerable distance outwards. The head-fold has been carried sufficiently far back to have resulted in the formation of a short rudiment of the fore-gut (plate XIII. figs. 15-17.). The notochord is distinguishable through a few sections only (plate XIII. fig. 18) as a median rounded group of cells, having exactly the character of

the mesoblast cells of the lateral plate. Without examining series of sections of a somewhat earlier stage than this it would be impossible to say positively that the notochord does not here arise from the hypoblast, but from the mesoblastic portion of the lower layer after the hypoblast has become separated from it as a definite layer of flattened cells: yet the similarity in character between the cells constituting this early rudiment of the notochord, together with the special character of the hypoblast cells and the absence of any transition forms between the two, would seem to strongly favour such a supposition.

There is no demarcation in the series of sections between the medullary groove and the primitive groove—the one passing insensibly into the other (plate XIV. fig. 19.). Where the axial groove becomes shallower behind the head-swelling the axial part of the mesoblast becomes continuous with the epiblast at the bottom of the groove and with the hypoblast below; and this coalescence of the three layers alone marks the passage from the embryonic region to the region of the primitive streak (fig. 20.). At its posterior end the primitive streak is elevated in the form of a ridge along the middle of the anterior part of which runs the primitive groove. In this region there are still only two layers—upper and lower.

In the next stage examined (plate IX. fig. 4) (in which, however, incubation had only gone on for 69 hours) the blastoderm was about five centimetres in diameter, the head-fold had become considerably further advanced, the medullary groove had become greatly increased in length, and the medullary folds much more prominent, though they had not yet begun to unite, and were only closely approximated in the cephalic region. There are five pairs of protovertebræ. At this stage there is no appearance of a neurenteric canal; the notochord passes directly behind into the substance of the axial plate, which is still of considerable extent. There is no mesoblast in the region in front of the head. The head-folds of the splanchnopleure have become united in the region of the head to form a short fore-gut. In the diverging splanchnopleure folds there is yet no rudiment of the heart.

A comparison of this blastoderm with the preceding one, and a comparison of corresponding stages in the fowl will show that the notochord extends backwards much more rapidly than the whole embryonic region *plus* the primitive-streak region increases in size. This it can only do at the expense of the cells of the axial plate, with which it is continuous behind. Since, however, the notochord is never found to extend backwards in this axial plate, it follows that as the former grows backwards the cells of the latter become detached from the epiblast and spread out, so as to resemble in their arrangement the mesoblast cells in front of them. There is in this way a progressive separation from before backwards of the deeper part of the axial plate from a surface layer of epiblast. Thus, in a sense, the primitive streak takes part in the formation of the hinder part of the embryo, becoming at the same time gradually reduced, till it occupies at last only an extremely small space at the posterior end of the embryo. In this manner the anterior part of the primitive streak becomes the posterior part of the medullary plate, and the primitive groove in its anterior part is not separate from the medullary groove, and really becomes converted into the posterior part of the latter. This will account for the great length of the primitive streak; it does not entirely represent the coalesced lips of the blastopore, but the anterior part is the foundation of the embryonic area.

This is substantially the same as Kölliker's\* account of the origin and history of the notochord and the destiny of the primitive streak in the chick; and Braun† gives a similar account for the *Melopsittacus*. It is not, however, that given by the majority of embryologists, who differ greatly not only as to the mode of formation of the chorda, but as to its subsequent mode of growth, and the share which the primitive streak has in further development.‡

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\* XXIV.

† X.

‡ See the memoirs of Balfour, Hoffmann, and Gerlach cited below. For a summary of opinions as to the part taken by the primitive streak in the formation of the embryo, see Kölliker, XXIV, pp. 134-138.

In the next stage observed, the head has become distinctly folded off, there is a rudiment of the tail-fold, and there are two pairs of protovertebræ; the anterior or cephalic fold of the amnion is rising up around the head, and the caudal fold is distinguishable, though not prominent. The neural canal is closed throughout except a very small portion at the posterior end; the cerebral vesicle presents no trace of subdivision, and the medullary canal is not prolonged backwards as it is at a subsequent stage.

The next stage (plate X, fig. 5) was from an egg which had been incubated for sixty-five hours. The whole blastoderm was seven and a half centimetres in diameter. The medullary canal was closed throughout, the primary vesicles of the brain distinguishable, with rudiments of the optic vesicles and a commencing division of the hind-brain into two.

In an embryo of ninety-four hours, which corresponds very closely with a thirty-six hours' chick, there are sixteen pairs of protovertebræ and the primary vesicles of the brain are distinguishable; the heart has the form of an S-shaped tube, and "blood-islands" have begun to make their appearance on the future vascular area. The medullary canal is nearly completely closed; behind (plate X. fig. 6) it is continued backwards in the form of a pear-shaped structure—the remains of the primitive streak, such as is often to be seen in a corresponding stage in the chick. At this point, as is seen from sections, the notochord terminates by becoming merged in what remains of the primitive streak; the hinder end of the medullary canal sends a short prolongation downwards into the mass of cells constituting the remains of the primitive streak, but this downward prolongation is short and ends blindly below. It is the only representative of the *neurenteric canal* found at a later stage. Behind it the three layers are all united in the middle line for a short distance.

There is still only a very thin layer of mesoblast in the region in front of the head. The fore-brain presents the merest rudiments

of optic lobes, and its ventral wall is still incompletely united along the middle line. The intermediate cell mass is very clearly distinguishable, but there is as yet no indication of the Wolffian duct. The notochord is continuous behind with the floor of the medullary canal; at this point it is continuous with the hypoblast at the sides.

In an egg which had been incubated for a hundred and eighteen hours, the blastoderm was found to be about seven and a half centimetres in diameter; the vascular area, still without developed blood-vessels, was eight millimetres in length, thus being smaller than the last. There were nineteen protovertebræ. The heart and splanchnopleure folds were not further advanced in development; the optic lobes had just begun to bud out, and the amnion invested the whole head end of the embryo. The neurenteric canal is not yet distinguishable. From the hinder end of the medullary canal (plate X. fig 7) there leads backwards a narrow passage which opens on the surface by a rounded opening close to the posterior termination of the area pellucida. In front of the opening are two unsymmetrical rounded lobes. Just behind the posterior end of the notochord there is a complete continuity between the three germinal layers.

In an embryo of a hundred and fifteen hours (plate XI. fig. 8) the blastoderm was found to have spread over about a third of the yolk; the vascular area, which was twelve millimetres in length, was marked with numerous 'blood-islands'; the area pellucida was 7 mm.; there were twenty-four pairs of protovertebræ, and the cranial flexure was beginning to be distinct; the optic vesicles were prominent, and the head of the embryo was beginning to be turned, so as to lie on the left side.

The posterior end of the neural axis exhibited very nearly the same general appearance as in the preceding stage, but the pear-shaped vesicle terminated more abruptly behind. Some little distance in

front of this there is a very distinct neurenteric canal, which is readily discernible when the embryo is looked at from the ventral aspect. In front of it, where the notochord ends posteriorly, there is a complete continuity of epiblast, mesoblast, and hypoblast, and the notochord is continuous with the hypoblast.

As will be seen from the series of sections figured (plate XIV. figs. 21-23), the passage is a very direct and open one, leading from the posterior end of the completely closed neural canal behind the extremity of the notochord (*n. ch.*) into the enteric cavity. The wall of the passage has the same structure as that of the neural canal, but the passage cannot be regarded as strictly a bending downwards of the posterior end of the neural canal, the latter being continued backwards behind it, though only for a very short distance. At this stage the notochord has become separated from the mesial thickening of the primitive streak, with which it was at first continuous, by the intervention of the neurenteric canal, and its posterior end appears as a thickening of the hypoblast. It remains separate from the floor of the medullary canal, in front of the neurenteric passage, though it may be said to pass into it round the sides of the latter.

An embryo of a hundred and twenty-one hours, though incubated for three hours longer than that just described, had apparently scarcely attained the same stage of development, since the posterior end of the medullary axis presented exactly the same appearance as in the case of the embryo of a hundred and fifteen hours; and there was an evident, though very narrow, neurenteric canal.

The neurenteric canal above described is the equivalent of that first described by Gasser in the goose, and subsequently noticed by Balfour and by Hoffmann in the chick, of the first (more anterior) of those described by Braun in the duck and the wagtail, and of the one described by the same author in the pigeon and fowl and in *Melopsittacus undulatus*.

The only later stage examined was an embryo of seven days, which had attained to about the same grade of development as a 60 hours' chick, with well developed vascular area, heart bent upon itself, visceral arches and clefts, cranial flexure well marked, lens-involution still connected with the epiblast, auditory sac still opening on the exterior, and with the amnion completely covering the whole surface with the exception of a small key-hole-shaped aperture above the posterior end of the medullary canal.

In this specimen (plate XV, figs. 24-28) there is in the caudal region, just behind the posterior end of the notochord a passage (neurenteric canal) from the hinder end of the medullary canal to the hind gut. This corresponds in position to the neurenteric canal already described at a much earlier stage ; but whether it is the same canal or a fresh formation is uncertain. It is the equivalent seemingly of a canal which has sometimes been observed in the fowl in the middle of the third day of incubation.\*

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#### LITERATURE.†

- I.—BALFOUR, F. M. A Treatise on Comparative Embryology.
- II.—BALFOUR, F. M., AND FOSTER, M. Elements of Embryology.
- III.—BALFOUR, F. M., AND F. DEIGHTON. A renewed Study of the Germinal Layers of the Chick. *Quart. Journ. Micro. Sci.* XXII., 1882, and *Studies from the Morph. Lab. of Cambridge University* ; and *Works, Memorial Edition, Vol. I., p. 854.*
- IV.—BALFOUR, F. M. The Development and Growth of the Layers of the Blastoderm. *Q. J. Micro. Sci.* XII., 1873 ; and *Works, Memorial Edition, Vol. I., p. 29.*

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\* Rauber, XXIX. p. 147.

† This is not intended as a complete bibliography, including as it does only such works and papers bearing on the subject as I have been able to consult. In a good many instances in which the publications are not represented in Sydney Libraries, I have gained a general knowledge of their contents from the abstracts in the 'Zoologischer Jahresbericht,' and as I have had to refer to these, I have entered them, adding the number of the volume of the 'Jahresbericht' in parenthesis.

- V.—BALFOUR, F. M. On the Disappearance of the Primitive Groove in the Embryo Chick. Q. J. Micro. Sci. XIII, 1873; and Works, Memorial Edition, Vol. I., p. 41.
- VI.—BALFOUR, F. M. A Comparison of the Early Stages in the Development of Vertebrates. Q. J. Micro. Sci. XV., 1875; and Works, Memorial Edition, Vol. I., p. 112.
- VII.—BALFOUR, F. M. On the Early Development of the Lacertilia, together with some Observations on the nature and relations of the primitive streak. Q. J. Micro. Sci. XIX., 1879, and Works, Memorial Edition, Vol. I., p. 644.
- VIII.—BELLONCI, G. Blastoporo e linea primitiva dei Vertebrati. Atti Accad. Linc. Mem. (3). Vol. 19. [Abstract in Zool. Jahresber., 1884, IV.]
- IX.—BRAUN, M. Aus der Entwicklungsgeschichte der Papageien. Bericht d. 52 Vers. deutsch. Naturf. u. Ärzte zu Baden-Baden (1879), and Verh. Phys. Med. Ges. Würzburg, 14 Bd. (1880). [Abstracts in Zool. Jahresb., 1879, II., and 1880, IV.]
- X.—BRAUN, M. Die Entwicklung des Wellenpapageies (*Melopsittacus undulatus*). Arbeit. a. d. Zool.-Zoot. Institut zu Würzburg, V. [Abstracts in Zool. Jahresb., 1879, II., and 1881, IV].
- XI.—DISSE, J. Die Entwicklung des mittleren Keimblattes im Huhnerei. Arch. f. mikr. Anat. XV. (1878).
- XII.—DUVAL, M. De la formation du blastoderme dans l'oeuf d'Oiseaux. Ann. des Sciences Nat. Zool. (6me série), tome 18 (1884).
- XIII.—DUVAL, M. Étude sur la ligne primitive de l'embryon du poulet. Ann. Sci. Nat. VII. (1879).
- XIV.—GASSER, R. Der Parablast u. der Keimwall der Vogelkeimscheibe. Sitz. Ber. Nat. Ges. Marburg, Nr. 4. [Abstract in Zool. Jahresber., 1883, IV., p. 136].
- XV.—GASSER, E. Beiträge zur Kenntnis der Vogelkeimscheibe. Arch. f. Anat. u. Phys. 1882. Anat. Abth. 4/6 Heft, p. 359-398. [Abstract in Zool. Jahresber., 1882, IV.]
- XVI.—GERLACH, L. Die entodermale Entstehungsweise der Chorda dorsalis beim Hühnchen. Biol. Centralbl. I. Nr. 1, pp. 21-25 and Nr. 2, pp. 38-49.

- XVII.—GOETTE, A. Beiträge zur Entwick. der Wirbelthiere, II. Die Bildung der Keimblätter und des Blutes im Hühnerei. Arch. f. mikr. Anat. X. (1874).
- XVIII.—HENSEN, V. Embryologische Mittheilungen. Arch. f. mikr. Anat. III. (1867).
- XIX.—HOFFMANN, C. K. Ueber die Entwicklungsgeschichte der Chorda dorsalis. Festschrift für Henle. [Abstract in Zool. Jahresber., 1882, IV].
- XX.—HOFFMANN, C. K. Die Bildung des Mesoderms, die Anlage der Chorda dorsalis und die Entwicklung des Canalis neurentericus bei Vogelembryonen. Verh. Akad. Amsterdam, Deel 23. [Abstract in Zool. Jahresber., 1883, IV., p. 137].
- XXI.—JANOSIK, J. Beitrag zur Kenntnis des Keimwulstes bei Vögeln. Sitzungsber. Wien. Acad. 84 Bd., 3 Abth. [Abstract in Zool. Jahresber., 1882, IV].
- XXII.—KOLLER, C. Untersuchungen üb. d. Blätterbildung im Hühnerkeim. Arch. für mikr. Anat. XX. (1882).
- XXIII.—KOLLER, C. Beiträge zur Kenntniss des Hühnerkeims im Beginn der Bebrütung. Sitzber. d. Wien. Akad. d. Wissensch. 1879. [Abstract in Zool. Jahresber., 1880, IV].
- XXIV.—KÖLLIKER, A. Entwicklungsgeschichte des Menschen und der höheren Thiere. Leipzig, 1879.
- XXV.—KUPFFER, K. Die Gastrulation an den meroblastischen Eiern der Wirbelthiere und die Bedeutung des Primitivstreifens. Arch. f. Anat. u. Phys. 1882, Anat. Abth 2/3 Heft. [Abstract in Zool. Jahresber., 1882, IV].
- XXVI.—KUPFFER, K. Die Entstehung d. Allantois u. d. Gastrula d. Wirbelthiere. Zool. Anz., II. (1879).
- XXVII.—OELLACHER, J. Beiträge zur Geschichte des Keimbläschens im Wirbelthierei. Archiv f. mikr. Anat. VIII.
- XXVIII.—RAUBER, A. Primitivrinne u. Urmund. Morph. Jahrb. v. Gegenbaur, II. (1876).
- XXIX.—RAUBER, A. Noch ein Blastoporus. Zool. Anz. VI., pp. 143-147, 163-167.
- XXX.—RAUBER, A. Die Lage der Keimpforte. Zool. Anz. II. (1879).

- XXXI.—SPOOF, A. R. Beiträge zur Embryologie u. vergleichenden Anatomie der Kloake u. Urogenitalorgane bei den höheren Wirbelthieren. [Abstract in Zool. Jahresber., 1883, IV., p. 140].
- XXXII.—WHITMAN, C. O. On a rare form of the Blastoderm of the Chick. Quart. Journ. Micro. Sci. Vol. XXIII.
- XXXIII.—WIJHE, A. VAN. Ueber den vorderen Neuroporus und die Phylogenetischen Function des Canalis neurentericus der Wirbelthiere. Zool. Anzeiger VII.
- XXXIV.—WOLFF, W. Ueber die Keimblätter des Huhnes. Archiv f. mikr. Anat. XXI. (1882).

## EXPLANATION OF PLATES.

## PLATE VIII.

- Fig. 1.—Blastoderm of emu after 70 hours' incubation, with well-advanced primitive streak and primitive groove (*pr.*) on a narrow posterior prolongation (*p.*) of the area pellucida (*ap.*) The letter *h.* points to the slightly convex anterior border of the mesoblast extending forwards towards the region of the future head of the embryo. *ao.* area opaca. From fresh specimen.
- Fig. 2.—Blastoderm of 66 hours; rather further advanced than the preceding; the posterior prolongation of the area pellucida no longer sharply marked off from the rest, a crescentic groove (*h.*) marking the anterior limit of the mesoblast and of the medullary plate (*m.p.*). *pr.* primitive streak and groove. From prepared specimen.

## Plate IX.

- Fig. 3.—Blastoderm of 78 hours, with advanced head-fold (*h.*) and rudimentary medullary groove and medullary folds (*m.*). From fresh specimen.
- Fig. 4.—Blastoderm incubated for 69 hours, considerably further advanced than that represented in fig. 3, with well-marked head (*h.*) and five pairs of protovertebræ. The medullary folds have become prominent and have almost met in the middle region of the head: the primitive groove is still of considerable extent. *h.a.* head-fold of amnion. *Sp.* splanchnopleure. From prepared specimen.

Plate x.

Fig. 5.—Embryo of 65 hours with eleven pairs of protovertebræ and developing vascular area. The vesicles of the brain have become differentiated, with slight rudiments of the optic vesicles of the fore-brain (*f.b.*), the hind-brain (*h.b.*) beginning to divide into two parts. The cleft in the fore-brain has become artificially enlarged. *ht.* heart. *v.* vitelline vein.

Fig. 6.—Hinder part of embryo of 94 hours, with seventeen pairs of protovertebræ. *pr.* remains of primitive streak.

Fig. 7.—Hinder part of embryo of 118 hours with nineteen pairs of protovertebræ, in which there is a narrow canal leading from the posterior end of the medullary canal and opening by a small pore (*o.*) on the surface. From fresh specimen.

Plate xi.

Fig. 8.—Embryo of 115 hours with twenty-four pairs of protovertebræ, with well-developed optic vesicles and S-shaped heart. The dark spot (*n.*) marks the position of the neurenteric canal. *pr.* hinder end of remains of primitive streak. From fresh specimen.

Plate xii.

Fig. 9.—Transverse section of blastoderm with a rudimentary primitive streak (incubated for 51 hours) in the anterior part of the primitive streak, showing union of upper and lower layers in their thickened middle part. *ep.* epiblast. *hy.* developing hypoblast cells. *ms.* lower layer cells which will become converted into stellate mesoblast.

Fig. 10.—Transverse section of 70 hours' blastoderm (fig. 1), passing through the head process. *ep.* epiblast. *l.* lower layer cells of head process, some of which are being converted into stellate mesoblast cells, and others (*hy.*) into flattened hypoblast cells. *n.* nutrient corpuscles.

Fig. 11.—Section of the same blastoderm at the anterior end of the primitive streak. *ep.* epiblast. *ms.* mesoblast cells developed from lower layer (compare with fig. 9). *hy.* hypoblast cells. *n.* nutrient corpuscles.

Fig. 12.—Section of the same a little further back, with complete hypoblast layer (*hy.*)

Fig. 13.—Section of the same showing secondary cleft in primitive streak.  
*pr.* primitive groove. *ms.* mesoblast. *ep.* epiblast. *n.* remarkable granular cell in hypoblast below the cleft.

## Plate XIII.

Fig. 14.—Section of the same at the extreme posterior end of the primitive streak.

Fig. 15.—Transverse section through the head-swelling of embryo of 78 hours (fig. 3). *mg.* anterior part of medullary groove. *ep.* epiblast. *ms.* mesoblast. *fg.* commencing fore-gut.

Fig. 16.—Section of the same a little further back ; letters as before.

Fig. 17.—Central part of the same section more highly magnified.

Fig. 18.—Section of the same blastoderm passing through the hinder part of the medullary plate, with the rudimentary notochord (*n. ch.*) separated from the lateral plates of mesoblast (*ms.*).

## Plate XIV.

Fig. 19.—Section showing the transition from the medullary plate to the region of the primitive streak : the notochord (*n.ch.*) passing into the axial plate.

Fig. 20.—Section a little further back behind the termination of the notochord.

Fig. 21.—Section of 115 hours' embryo (fig. 8) just in front of the neurenteric canal, showing the continuity of the hypoblast (*hy.*) with the notochord (*n.ch.*) at this point. *m.* medullary canal.

Fig. 22.—Section of the same a little further back, passing through the neurenteric canal.

Fig. 23.—Section of the same embryo a little behind the neurenteric canal.  
Letters as before.

Plate xv.

Figs. 24—28 are a series of sections through the hinder end of a seven days' embryo showing the neurenteric passage, and the relation of the hinder end of the notochord at this stage to the hypoblast of the hind gut.

Fig. 24.—Section just in front of the neurenteric canal, with separate hind gut (*hg.*), notochord (*n. ch.*), and medullary canal (*m.*). *ms.* lateral plates of mesoblast. *am.* amnion.

Fig. 25.—Section a little further back at a point where the notochord has united with the wall of the hind gut.

Fig. 26.—Section showing union of wall of hind gut and of medullary canal.

Figs. 27 and 28.—Sections passing respectively through the anterior and the posterior parts of the neurenteric passage.